

# Distribution and Changes in Abundance of *Ailanthus altissima* (Miller) Swingle in a Southwest Ohio Woodlot

AMANDA L. ESPENSCHIED-REILLY<sup>1</sup> AND JAMES R. RUNKLE. Department of Biological Sciences, Wright State University, 3640 Colonel Glenn Highway, Dayton, OH 45435

**ABSTRACT.** This study describes the population structure and dynamics of *Ailanthus altissima* within the Wright State University woodlot near Dayton, Ohio. This 80 ha woodlot contains both old growth and secondary stands. *Ailanthus altissima* populations were measured first in 1980 and again in 2001 and 2002. We examined changes in *A. altissima* demographics and patterns of occurrence by examining secondary environmental factors that could have influenced invasion and survival. *Ailanthus altissima* was found in 13.5% of the plots (500m<sup>2</sup> each) and had a density of 198.4 stems/ha, an increase from 1980. Although usually at low densities within the interior, occasional high density patches occurred. Tree cores dated the initial invasion of *A. altissima* before 1940. The number of *A. altissima* stems and the basal area of *A. altissima* decreased with increased distance from the woodlot edge. Percent annual survivorship was 42% overall and survivorship was negatively correlated with distance from the woodlot edge. Surviving understory stems have the potential to enter the canopy in the future. The presence of *A. altissima* along the woodlot perimeter was not related to aspect. *Ailanthus altissima* successfully invaded both the old and secondary growth sections of the woodlot, with its biggest influence on the woodlot edge, where it frequently dominated areas. A smaller presence in the woodlot interior is maintained presumably due to seedling success in canopy gaps and the formation of persistent clumps of clonal sprouts around canopy trees.

OHIO J SCI 108(2) 16-22, 2008

## INTRODUCTION

Exotic species have detrimental effects on native species and ecosystems and are one of the most important agents of habitat transformation in the world (Cronk and Fuller 1995; Richardson and others 2004). These effects can include direct competition with natives for resources and space, indirect competition via changing the food web or physical environment, allelopathic inhibition, or hybridization (Vitousek 1990; Westman 1990; Stein and Flack 1996). More than 5,000 introduced plant species have escaped and now exist in native habitats within the United States. Of this number, 138 are exotic trees or shrubs (Pimental and others 2000). Exotic plants cause environmental damage and losses totaling approximately \$34 billion per year in the United States. This figure excludes intangible losses, such as species extinctions and losses in biodiversity, ecosystem services, and aesthetics (Pimental and others 2000). While costs are alarmingly high, not all exotic plant species become naturalized within native habitats, and of those that do, only a small fraction cause ecological or economical problems (Crawley 1987; Vitousek 1990; Lodge 1993; Bright 1995). Unfortunately, there are no fail-safe methods for predicting which exotic plant species will become pest invaders or for predicting the effects of an exotic plant species on native species and ecosystems (Crawley 1987; Bright 1995). However, experimentation in plant invasion ecology has developed a set of generalizations that impact applications in invasion management (Richardson and others 2004).

An exotic species found across the United States is the tree-of-heaven, *Ailanthus altissima* (Miller) Swingle, family Simaroubaceae, order Sapindales. *Ailanthus altissima* is a native of central China (Xheng and others 2004). It was first brought to the eastern United States in 1784, via Europe, as an ornamental and an urban street tree because of its lush foliage and ability to thrive in various conditions (Illick and Brouse 1926; Hu 1979; Peigler 1993; Shah 1997). *Ailanthus altissima* was first planted in Philadelphia, but soon after was planted widely in many eastern cities and was introduced to the west coast during the California gold rush in the

mid 19<sup>th</sup> century. It thrived in cities when many other trees could not due to its high tolerance of pollution. *Ailanthus altissima* is highly pollution tolerant, although high ozone concentrations can cause foliar damage (Gravano and others 2003). By the latter half of the 19<sup>th</sup> century, *A. altissima* had invaded many natural habitats in the United States and was considered a pest species (Illick and Brouse 1926; Hu 1979; Peigler 1993; Shah 1997).

The Nature Conservancy recognizes *A. altissima* as an exotic weed of importance and the Ohio Department of Natural Resources recognizes *A. altissima* as a well-established invasive species (Hoshovsky 1999). *Ailanthus altissima* is a disturbance specialist that grows in a wide variety of habitats including forests, urban areas, reclaimed surface mines, along roads and highways, edges, and fields (Miller 1990; Peigler 1993). *Ailanthus altissima* is tolerant of drought, soil compaction, and soil temperatures up to 36°C, but is considered intolerant of shade (Rabe and Bassuk 1984; Pan and Bassuk 1985; Graves and others 1989; Miller 1990; Facelli and Pickett 1991; Lodge 1993; Kowarik 1995; Knapp and Canham 2000) although recent studies have found sizable populations of *A. altissima* in woodland interiors (Kowarik 1995; Knapp and Canham 2000; Bertin and others 2001).

Due to its shade intolerance, it is thought that *A. altissima* can not compete with native species in a forest environment (Knapp and Canham 2000). However, *A. altissima* has been found as a component of the canopy of several native forests. It is able to invade the forest interior by taking advantage of opportunities provided by disturbances resulting in forest canopy gaps, such as lightning strikes and treefalls. This is a gap-obligate invasion strategy (Orwig and Abrams 1984; Kowarik 1995; Knapp and Canham 2000). In addition, a recent study by Hammerlynck (2001) indicates that *A. altissima* sprouts can maintain a positive energy balance even in shaded conditions. It is not only the clonal root sprouts that can be a threat to native forests, but also the seedlings of *A. altissima*. *Ailanthus altissima* is an effective long distance disperser of seeds, even in forested habitats (Kota 2005). It can maintain a seed bank for at least a year and it has a germination advantage over *Liriodendron tulipifera*, although *L. tulipifera* seedlings have a higher survival rate (Kota 2005; Kota and others 2006). In a recent study comparing

<sup>1</sup>Corresponding author currently at Mount Union College, 1972 Clark Ave., Alliance, OH 44601, espensal@muc.edu.

characteristics of 26 species of trees varying in invasiveness, *A. altissima* was categorized as more highly invasive due to its high relative growth rate and specific leaf area (Grotkopp and Rejmanek 2007). These studies indicate the importance of research that examines the community and population dynamics of *A. altissima* within wooded areas over longer periods of time.

The objectives of this study were to describe the population structure and dynamics of *A. altissima* within the Wright State University (WSU) woodlot near Dayton, Ohio. *Ailanthus altissima* is the only non-native tree species well established in this woodlot, and it is therefore important to determine why it has been successful. The specific questions we addressed were 1) Is *A. altissima* more abundant along the edge or within the interior of the woodlot? 2) Is *A. altissima* more abundant in the old or secondary growth stands? 3) Along the woodlot edge, does *A. altissima* abundance vary with aspect? 4) In the interior, does *A. altissima* abundance depend on stand age and tree density? 5) Is *A. altissima* present in all size classes from seedlings to canopy trees? 6) Have canopy individuals established at different times, suggesting that recruitment into the canopy has been ongoing? 7) Has density remained constant since 1980? 8) What is the annual survivorship of *A. altissima*?

## METHODS

### Study Area

This study was conducted within the Wright State University woodlot located near Dayton in Greene County in southwestern Ohio at latitude 39° 45'N and longitude 84° 3'W. The climate is classified as continental (DeMars and Runkle 1992). The average Ohio temperatures for January and July for 1992–2002 were -1.9°C and 22.8°C, respectively. The average annual precipitation for Ohio for 1992–2001 was 99 cm (NOAA 2002). The study area soils are Miamian silt-loams (Garner and others 1978).

The WSU woodlot is approximately 80 ha and includes three major stands (DeMars and Runkle 1992). Two of these are secondary growth and are derived from agricultural fields abandoned in 1935 and 1955. Dominant tree species in these stands include slippery elm (*Ulmus rubra*), white ash (*Fraxinus americana*), hackberry (*Celtis occidentalis*), sugar maple (*Acer saccharum*), and black cherry (*Prunus serotina*). These secondary stands are unusual in Ohio because of their high dominance by black locust (*Robinia pseudo-acacia*), a species only found in Ohio's southern counties (Runkle and others 2005). The third stand has never been clear cut, although some selective cutting and livestock grazing did occur up until 1950. This stand is dominated by white oak (*Quercus alba*), red oak (*Q. rubra*), black walnut (*Juglans nigra*), sugar maple, white ash, slippery elm, basswood (*Tilia americana*), black cherry, bitternut hickory (*Carya cordiformis*), and shagbark hickory (*C. ovata*) (Runkle and others 2005). This stand is classified as a changing old growth stand (Runkle 1996), in transition toward fewer oak and more sugar maple (Runkle and others 2005). Braun (1950) included Greene County in the beech-maple (*Fagus-Acer*) forest region. However, the WSU woodlot fits into Gordon's (1969) community classification as oak-sugar maple. DeMars and Runkle (1992) studied relationships among the ground layer vegetation, soil factors, topographic position, and stand age. Basal areas for all stands were about 30 m<sup>2</sup>/ha in 2000 (Runkle and others 2005).

### Transects

Initial estimates of *A. altissima* population structures were made in 1980. The second author, Runkle, sampled woody species

in the WSU woodlot using two techniques for different parts of the woodlot. First, he used contiguous plots along line transects placed 50 m apart and beginning at the woodlot edge. Stems  $\geq 9$  cm dbh were sampled in plots 5 m long (along the transects) by 8 m wide. Stems  $\geq 0.5$  m high and  $< 9$  cm dbh were sampled in plots 5 m long by 4 m wide. Stems  $< 0.5$  m high were sampled in two 1 m<sup>2</sup> quadrats along the center of the transect line in each 5 m section of that line, corresponding to the larger plots listed above. Altogether, 1,071 plots (nested plots for all sizes) were sampled. Second, he sampled a different section of the woodlot using 150 circular plots with concentric subplots. Stems  $\geq 4.5$  cm dbh were sampled in a 250 m<sup>2</sup> circle. Stems  $\geq 0.5$  m high and  $< 4.5$  cm dbh were sampled in a 25 m<sup>2</sup> circle. Stems  $< 0.5$  m high were sampled in a 2.5 m<sup>2</sup> circle. From this earlier study, only data on *A. altissima* were included in our current analysis.

In 2002, the abundance of *A. altissima* within the woodlot interior was determined using transects running through the woodlot beginning at the woodlot edge. Transects were laid out perpendicular to the woodlot edge. Along the transects, a series of 500 m<sup>2</sup> (diameter = 25.2 m) circular plots were established. The distances between these plots along one transect and between transects were 40–100 m, as determined by using a random number table. These distances were chosen in order to sample about 10% of the total woodlot interior.

Each circular plot was identified as being part of the old or secondary growth stands. All *A. altissima* stems found within a plot were counted and assigned into size classes: 1 = stems  $< 30$  cm in height were considered seedlings or small clonal sprouts, 2 = stems 30–133 cm (saplings), 3 = stems  $\geq 134$  cm, but not a canopy tree (subcanopy), and 4 = any canopy tree. Diameter at breast height (dbh) measurements were taken for all *A. altissima* stems 134 cm or taller. Any *A. altissima* stems with dbh measurements of 10 cm or more were cored using an increment borer and subsequently aged. We cored any *A. altissima* stems of this size that we found along the transects, including those outside of the circular plots, in order to increase the sample size for age analysis.

Data collection from 2002 and 1980 was not coordinated in advance because the idea to compare this study to the 1980 study was conceived after the 2002 field work was completed. This difference in sampling techniques resulted in somewhat different sized *A. altissima* individuals being included in each size class. For the 1980 study, the comparable size classes were: 1 =  $< 0.5$  m in height (seedlings or small clonal sprouts), 2 =  $> 0.5$  m high, but  $< 0.5$  cm dbh (saplings), 3 =  $\leq 25$  cm dbh (subcanopy), and 4 =  $> 25$  cm dbh (canopy). Although these size classes are not exactly the same, based on our experience at the site, we are confident that they are close enough to be comparable.

### Macroplots

In summer 2001 four 50 x 50 m macroplots were established; two in the old growth sections of the WSU woodlot (O1 and O2) and two in the secondary growth sections (S1 and S2). Macroplots were used to examine the relationship between *A. altissima* population density and distance from the woodlot edge, as well as the annual understory survival rate of *A. altissima*. Suitable areas for macroplots were determined by identifying all perimeter plots (discussed below) with  $\geq 50\%$  *A. altissima* coverage, which was estimated visually. Perimeter plots near areas of the woodlot containing large trails or areas that were not large enough to contain a macroplot were discarded and the final sites were chosen randomly from the remaining suitable sites. The outer edges of the macroplots were

subjectively located just inside the dense tangle of lower stems that characterized the outer edges of the woodlot.

Macroplots were divided into 25 10 x 10 m subplots (Fig. 1). Associated with each macroplot were five edge plots. These plots were all 10 m wide, but of varying lengths extending from the macroplot to the woodlot edge.

Within each subplot, including edge plots, all *A. altissima* stems were counted, tagged, and assigned one of the same size classes as described for the transects. Diameters were measured on trees reaching breast height (134 cm) and all *A. altissima* with a dbh  $\geq$  10 cm were again cored and aged. Within all subplots, excluding the edge plots, all woody stems of other species  $\geq$  10 cm dbh were measured and identified.

In order to determine the annual mortality of the tagged understory *A. altissima* stems we resampled three of the macroplots (O1, O2, and S2) in mid July 2002. All living tagged stems were relocated, counted, and assigned a size class. S1 was not resampled because it had been cut back and sprayed.

### Perimeter Plots

In June 2001 we divided the perimeter of the woodlot into 220 perimeter plots that were each 25 m long and 2 m deep. If *A. altissima* was present, we visually estimated the fraction of the foliage that was *A. altissima* with the aid of a meter tape. These observations were assigned into percent coverage classes: 0 = not present, 1 = 1–24%, 2 = 25–49%, 3 = 50–74%, 4 = 75–100%. Aspect and stand age were also determined for each perimeter plot.

### Statistical Analysis

For the transect plots, chi-squared tests compared similarities in the frequency of occurrence of *A. altissima* for the old and secondary growth woodlots. Linear regression was used to test for relationships between dbh and age for all cored *A. altissima*.

Spearman's rank correlation test was used in order to examine relationships between all variables examined in the macroplot study. Variables included distance from the woodlot edge, number of *A.*

*altissima* stems, basal area of *A. altissima* stems, number of stems of other woody species, basal area of other woody species, and annual survival of tagged *A. altissima* stems. Spearman's test was used because it is less influenced by outliers than correlation procedures based on the original data (Zar 1999). Simple regression analysis was used in order to relate annual survivorship of *A. altissima* to distance from the woodlot edge for the macroplots O1, O2, and S2. ANOVA was used to determine whether the number of stems and basal area of *A. altissima* varied among the two stand ages examined.

In order to look for significant differences between the frequency of occurrence of *A. altissima* along the perimeter and in stands of different ages and plots of different aspect the chi-squared test was used. Because relatively few perimeter plots contained *A. altissima* with a relatively high percent coverage, we considered *A. altissima* to be in one of two classes: present or not present. All statistical analyses were performed with PC SAS (Version 8.0, SAS Institute, Cary, NC) using a significance level of  $\alpha=0.05$ .

## RESULTS

### Stem Density and Frequency

The total density and the density per size class for the transects are shown with and without an outlier (Table 1). The outlier was one circular plot with an unusually high number of small *A. altissima* seedlings. Smaller understory *A. altissima* stems are more abundant than canopy trees and abundance decreases for each larger size class (Table 1). When compared with the densities from the 1980 sample, *A. altissima* density totaled from all size classes has increased from 21–42 stems/ha to 198 stems/ha. Individually all four size classes show an increase in *A. altissima* density over time, with the greatest increases in the smaller, or understory stems (Table 1).

The frequency (number of transect plots with *A. altissima* divided by the total number of transect plots) of *A. altissima* throughout the woodlot is 13.5%. The secondary and old growth stands did not differ significantly in *A. altissima* frequency (chi – square = 0.06, df = 1,  $p > 0.05$ ). Stand age had no significant effects on *A.*

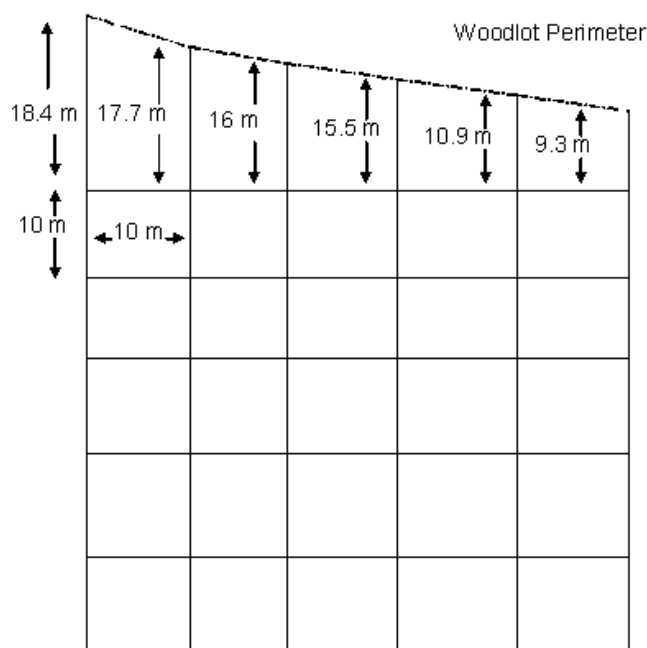


FIGURE 1. The layout for the O2 macroplot. This design was typical for all four macroplots.

Table 1

Comparison of transect densities of *Ailanthus* stems for 1980 and 2002. Size classes for 1980 are 1 = < 0.5 m in height, 2 = > 0.5 m in height, but < 0.5 cm in diameter at breast height (dbh), 3 = 0.5 – 25 cm dbh, and 4 = > 25 cm dbh. Comparable size classes for 2002 are 1 = stems < 30 cm in height, 2 = stems 30 – 133 cm in height, 3 =  $\geq$  134 cm in height, but not a canopy tree, and 4 = canopy tree. All values are in stems/ha.

Size Class	1980 (line plot)	1980 (circle plot)	2002
1	14	26.7	46.3, 639.8*
2	3.3	13.3	113.5
3	3.8	1.9	37.1
4	0	0.5	1.57
Total	21	42	198.4, 791.9*

\* indicates the mean with the inclusion of an outlier, a transect plot with an unusually high density of small seedling *Ailanthus*.



*altissima* stem density for any part of this study. Overall, we found 14.9 *A. altissima* stems/100 m<sup>2</sup> in the old growth macroplots (O1 and O2) and 11.6 stems/100 m<sup>2</sup> in the secondary growth macroplots (S1 and S2). *Ailanthus altissima* was found in 32% of the 225 perimeter plots (Table 2). Within these plots, *A. altissima* coverage was usually  $\leq 25\%$ , but was occasionally at 100%.

### Environmental Trends

The number of stems and basal area of *A. altissima* were negatively correlated with distance from the woodlot edge ( $p \leq 0.01$ ) (Table 3, Fig. 2A, 2B). *Ailanthus altissima* stem density and basal area were negatively correlated with the number of stems of other woody species ( $p = 0.01$  and  $p < 0.01$  respectively) and the basal area of other woody species ( $p = 0.02$  and  $p \leq 0.01$  respectively) (Table 3). The presence of *A. altissima* did not differ in perimeter plots of different aspect ( $p > 0.05$ ).

### Age and Survival Results

The mean absolute growth rate for the trees cored was 0.72 cm in diameter per year (Fig. 3). The oldest tree cored in the woodlot was 59 years old. The youngest canopy tree cored was 18 years old. The range of ages of the cored trees suggested that *A. altissima* has

gradually established itself within the canopy over the last 20 to 60 years.

Annual survivorship from 2001 to 2002 for all *A. altissima* found in the O1, O2, and S2 plots combined was 41.9%. *Ailanthus altissima* survival was negatively correlated with distance from the woodlot edge ( $p = 0.045$ ) (Table 3, Fig. 2C).

## DISCUSSION

The oldest *A. altissima* in the woodlot appears to be the 59-year-old canopy tree in the S2 macroplot. This dates the initial invasion of *A. altissima* before 1940, about the same time that part of the area was released from agriculture (DeMars and Runkle 1992). This date agrees with surveys of nearby Preble and Butler counties that list *A. altissima* as an occasional presence within forests about this same time (Byrd 1939; 1941). It is possible that *A. altissima* invaded or was planted earlier than 1940 with older trees already dead or not encountered during sampling. Since the normal lifespan of *A. altissima* is thought to be 50 to 70 years, several generations of canopy trees could already have passed since its establishment in the woodlot (Illick and Brouse 1926). Since the oldest tree was found in an area of secondary growth, *A. altissima* may initially have invaded younger stands and then spread to the old growth stand.

Table 2

The number and percent of perimeter plots that fall into each percent coverage class of *Ailanthus*.

Percent Coverage Classes	Number of Plots	Percentage of Plots
0	149	68
1-24	42	19
25-49	12	6
50-74	9	4
75-100	8	4

Table 3

Matrix of Spearman correlation values for variables used in the macroplot study.

Variables	<i>Ailanthus</i> Density	<i>Ailanthus</i> Basal Area	<i>Ailanthus</i> Survival
<i>Ailanthus</i> Density	---	0.67*	0.17
Basal Area	0.67*	---	0.62*
Density Other	-0.29*	-0.4*	-0.16
Basal Area Other	-0.22*	-0.32*	-0.09
Distance	-0.32*	-0.39*	-0.24*

\* indicates  $p < 0.05$ ;  $n = 116$  for all comparisons with the exception of those involving annual survival (2001-02), for which  $n = 48$ .

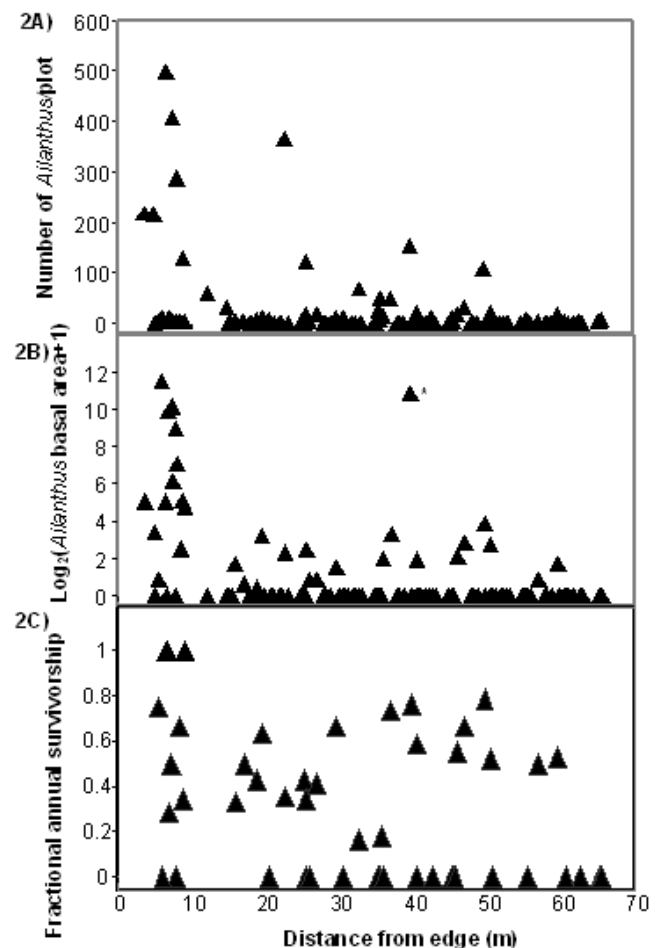


FIGURE 2. (A) The relationship between the number of *Ailanthus* stems per 100 m<sup>2</sup> plot and distance from the woodlot edge in all four macroplots.  $r = -0.32$ ,  $p < 0.05$ ,  $n = 116$  (B) Relationship between *Ailanthus* basal area and distance from the edge in all four macroplots.  $r = -0.39$ ,  $p < 0.05$ ,  $n = 116$ , \* indicates oldest *A. altissima* cored (C) Fractional annual (2001 – 2002) survivorship related to the distance from the woodlot edge for the O1, O2, and S2 macroplots.  $r = -0.24$ ,  $p < 0.05$ ,  $n = 48$ .

The two secondary growth stands were once fields, habitats easily colonized by pioneer species like *A. altissima* (Rabe and Bassuk 1984; Miller 1990; Facelli and Pickett 1991; DeMars and Runkle 1992; Kowarik 1995; Knapp and Canham 2000).

Even though the secondary growth stands were probably where *A. altissima* first invaded the woodlot, they do not differ from the old growth stand in terms of *A. altissima* stem density. Because *A. altissima* is considered a pioneer species, we were expecting to find it more frequently in the secondary growth sections of the woodlot. However, since *A. altissima* employs a gap-obligate invasion strategy, perhaps the formation of canopy gaps is more important than stand age for its distribution (Runkle 1996; Kowarik 1995; Knapp and Canham 2000). Since one of the secondary growth stands in the WSU woodlot is 70 years old, it may no longer offer advantages to the establishment of young trees and pioneer species compared with the older stand. Canopy gap processes also differ with stand age. Clebsch and Busing (1989) found that gaps in a second-growth stand in a Southern Appalachian cove forest were smaller in size, although more numerous than old growth canopy gaps. Old growth gaps contained higher light microsites because of their increased size, which can accommodate shade intolerant species, such as *A. altissima*. In addition, since *A. altissima* has been present within the WSU woodlot for at least 60 years, it may have had enough time to disperse into the old growth woodlot effectively. The old growth stand probably was disturbed by selective cutting and grazing in the past and this may have left it vulnerable to *A. altissima* invasion. Also, *A. altissima* may have established along the edges of the old growth stand, including edges now in the interior of the WSU woodlot as a whole. The distances from these former edges to the interior of the older woodlot were smaller than distances from the present woodlot edge. These former edges may have been the source of invasion of the old growth interior at the same time the secondary stands became established or earlier.

While presence of *A. altissima* did not differ between the secondary and old growth stands, it did differ between woodlot perimeter and interior. *Ailanthus altissima* is frequently found along the perimeter. This is not surprising considering that *A. altissima* has been well documented as a common species along edge habitats and in open spaces (Rabe and Bassuk 1984; Miller 1990; Facelli and Pickett 1991; Kowarik 1995; Knapp and Canham 2000). Exotic species are often increased in abundance near forest edge habitats, possibly due to increased resource availability or increased dispersal into forest edges (McDonald and Urband 2006). We expected *A. altissima* presence to vary along the edge due to aspect, occurring

more often along edges that received a greater amount of sunlight during the day, such as those facing south. *Ailanthus altissima* is reported to be a shade-intolerant species and to prefer areas with full sunlight (Rabe and Bassuk 1984; Miller 1990; Facelli and Pickett 1991; Kowarik 1995; Knapp and Canham 2000). However, we did not find this aspect to be significant. Instead, the distribution of *A. altissima* along the perimeter may be related to where *A. altissima* was initially introduced, disturbance history, or to its history of seed dispersal. The location of large canopy *A. altissima* may influence total edge *A. altissima*. Large canopy *A. altissima* are near many of the perimeter plots with a high percent coverage of *A. altissima* (Espenschied 2002). A canopy *A. altissima* can support hundreds of root suckers and can have roots ranging more than 8 m from its trunk (Illick and Brouse 1926; Davies 1935; 1944; Kowarik 1995). Thus, once one *A. altissima* has become established along the edge it can generate many new suckers after a few years. A female *A. altissima* can produce up to 325,000 seeds per year (Heisey 1997). The light, wind dispersed seeds can easily travel long distances and are readily germinated. Even though seedling survival can be relatively low (15.7% in one study), it is easy to see that one canopy female *A. altissima* could easily spread numerous seedlings in an area, as well as clonal root sprouts (Kota 2005).

*Ailanthus altissima* was also found within the woodlot interior, both in the macroplots and along the transects. While *A. altissima* can occur both along the woodlot perimeter and within the interior, the number of stems of *A. altissima* decreased with increased distance from the edge. Similarly, McDonald and Urband (2006) found that species composition along forest edges in North Carolina was significantly different than in the forest interior, but that this effect only penetrated about 5 m into the forest. We suspect that *A. altissima* first invaded along the Wright State woodlot as an edge species. Many of the canopy trees are near the forest edges. From the woodlot edge *A. altissima* could penetrate the interior via its wide ranging roots, effective long distance seed dispersal, and in gaps given its documented success as a gap colonizer (Davies 1944; Kowarik 1995; Knapp and Canham 2000; Kota 2005). The oldest tree cored was located in one of the secondary growth stands, which originated as farm fields. This and other interior canopy trees likely originated as edge individuals, becoming interior individuals due to the establishment of secondary stands around them as the old farm fields were abandoned.

*Ailanthus altissima* stems can sometimes be found at high densities within the interior of the WSU woodlot. With and without the outlier plot (Table 1), the density of *A. altissima* stems for all size classes has increased since 1980. The largest increase is in the smaller size classes. Relatively few *A. altissima* are present in the canopy, but canopy density has increased threefold since 1980 (Table 1). However, because understory clonal sprouts of *A. altissima* remain photosynthetically active at low irradiances and may receive aid in the form of resource reallocation from the parent tree, they can persist under the canopy for years, growing slowly, and awaiting a canopy disturbance (Kowarik 1995; Hammerlynck 2001), after which it is possible they could exploit the opportunity and outcompete native stems present for the available space (Kowarik 1995; Knapp and Canham 2000). However, a recent study found that *L. tulipifera* can outperform *A. altissima* in the first two years following a disturbance if sufficient viable seeds are present (Kota and others 2006). *Ailanthus altissima* can only maintain a seed bank for about one year (Kowarik 1995; Kota 2005). The seeds can germinate in low light conditions, but seedling mortality typically occurs within a year. Therefore, it is the clonal sprouts of

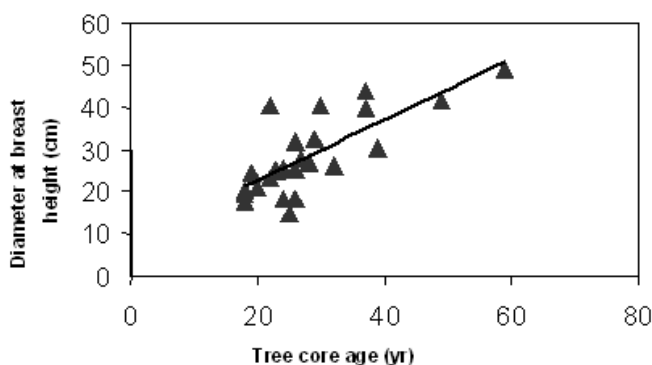


FIGURE 3. Relationship between diameter at breast height and tree age for canopy *Ailanthus* trees that were cored. The fitted equation is  $\text{dbh (cm)} = 0.7185\text{age} + 8.4105$ .  $\text{SD} = 0.24$ ,  $r^2 = 0.575$ ,  $n = 26$  trees,  $F_{1,24} = 32.4$ ,  $p < 0.01$ .

*A. altissima* that are the most likely to succeed in the understory and achieve canopy status (Kowarik 1995).

Some of the differences between the 1980 and the current results could be due to differences in techniques. The idea to compare this present study to the 1980 study was conceived after the recent field work was completed, which is the reason for the different field methods. The two samples used slightly different size classes. However, the fact that *A. altissima* increased in all size classes suggests that the increase is real. The two techniques sampled somewhat different sections of the woodlot, so some of the variation in results may be due to spatial differences in *A. altissima* density and not just to temporal differences.

Understory *A. altissima* are of concern only if they survive from year to year. All macroplots resampled contained understory *A. altissima* sprouts that had survived from 2000 to 2001, for a total of 42% survival. Most likely the stems that we found surviving were clonal sprouts. Kowarik (1995) found root suckers of *A. altissima* in a West Virginia forest ranging in age from one to 19 years. In contrast, the same researcher found 100% annual mortality in understory *A. altissima* seedlings. Another more recent West Virginia study found a 15.7% survival rate among *A. altissima* seedlings planted under a canopy (Kota 2005). While it has been shown that *A. altissima* can efficiently photosynthesize at low light levels (Hammerlynn 2001), clonal sprouts may have additional support via resource reallocation from the parent tree or even other larger sprouts nearby that give them an advantage over seedlings (Davies 1935; Kowarik 1995).

## CONCLUSIONS

*Ailanthus altissima* density increased within the WSU woodlot over the past twenty years (Table 1). The biggest increase was in the density of the understory stems, which could potentially become part of the canopy in the future. There was no difference in the presence of *A. altissima* between the secondary and old growth stands. While *A. altissima* probably first invaded in the secondary growth stands or along old woodlot edges it has spread into the old growth stand, both edges and interior.

The number of *A. altissima* stems decreased from the edge to the interior (Figure 2A). While *A. altissima* were found in the interior and occasionally in high density patches, it was more likely to be found in high densities near the woodlot edge.

The presence of *A. altissima* along the woodlot perimeter was not correlated with aspect. The presence of *A. altissima* along the perimeter was probably better explained by nearby canopy trees that can support numerous root suckers, areas of initial planting or invasion, and recent disturbance.

*Ailanthus altissima* was found in all size classes both in the macroplots and along the transects (Table 1). Survivorship was 42% for the three macroplots resampled. The surviving understory sprouts are likely to be primarily root sprouts.

In summary, *A. altissima* has successfully invaded both the old and secondary growth stands of the WSU woodlot. It has its biggest influence on the woodlot edge, frequently dominating local areas. A smaller presence in the woodlot interior is probably maintained due to occasional seedling success in canopy gaps and the formation of persisting clumps of clonal sprouts around canopy trees. Similar trends may be found in other woodlots with *A. altissima* and this study indicates that this invasive species has the ability to become naturalized within an area and should be a species that is targeted for removal. This study also demonstrates that *A. altissima* is capable of invading and maintaining a population within the interior of a

woodlot and not only along the exterior. This could indicate that *A. altissima* is capable of becoming an important invasive plant species within our native Eastern forests.

**ACKNOWLEDGEMENTS.** Thanks go to Wright State University and the Dayton Audubon Society for funding; to The New Company of Dover, OH for field supplies; to Bill Landers, Diem Tran, Tracey Wells, and Sara Basgier for assistance in the field; and to Drs. Don and Kendra Cipollini, Dr. James Amon, Dr. Richard Thomas, Dr. Skip Van Bloem, Dr. Clint Springer, Gera Jochum, and Sarah Briden for invaluable advice during the preparation of this manuscript.

## LITERATURE CITED

- Bertin RI, Cantwell T, Berstene B. 2001. Introduced tree species in urban woodlands in Worcester, Massachusetts. Annual Meetings of the Ecological Society of America 2001.
- Braun EL. 1950. Deciduous Forest of Eastern North America. Philadelphia (PA): Blakisten; Reprinted – 1972, Hafner Publ. 596 p.
- Bright C. 1995. Bio – invasions: The spread of exotic species. World Watch 8:10–19.
- Byrd JM. 1939. Forest resources of Preble County, Ohio. Forestry Publication No. 59. Wooster (OH): Ohio Agricultural Experiment Station, Division of Forestry. 34 p.
- Byrd JM. 1941. Forest resources of Butler County, Ohio. Forestry Publication No. 8. Wooster (OH): Ohio Agricultural Experiment Station, Department of Forestry. 49 p.
- Clebsch EEC, Busing RT. 1989. Secondary succession, gap dynamics, and community structure in a Southern Appalachian cove forest. Ecology 70(3):728–735.
- Crawley MJ. 1987. What makes a community invisable? Sym Brit Ecol Soc 26:429–453.
- Cronk QCB, Fuller JL. 1995. Plant Invaders: the threat to natural ecosystems. London: Chapman & Hall. 241 p.
- Davies PA. 1935. Ecology of *Ailanthus* thickets. Tran Kentucky Acad Sci 7:24.
- Davies PA. 1944. The root system of *Ailanthus altissima*. Trans Kentucky Acad Sci 11(3–4):33–35.
- DeMars BG, Runkle JR. 1992. Groundlayer vegetation ordination and site – factor analysis of the Wright State University woodlot (Greene County, Ohio). Ohio J Sci 92(4):98–106.
- Espenschied, AL. 2002. Environmental factors affecting *Ailanthus altissima* in the Wright State University woodlot. Masters Thesis, Wright State University, Dayton, OH. 78 p.
- Facelli JM, Pickett STA. 1991. Indirect effects of litter on woody seedlings subject to herb competition. Oikos 62:129–138.
- Gordon RB. 1969. The natural vegetation of Ohio in pioneer days. Bull Ohio Biol Sur 3:1–109.
- Gravano E, Giulietto V, Desotgiu R, Bussoti F, Grossoni P, Gerosa G, Tani C. 2003. Foliar response of an *Ailanthus altissima* clone in two sites with different levels of ozone-pollution. Environ Pollut 121:137–146.
- Graves WR, Dana MN, Joly RJ. 1989. Influence of root – zone temperature on growth of *Ailanthus altissima* (Mill.) Swingle. J Environ Hort 7:79–82.
- Grotkopp E, Rejmanek M. 2007. High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. Am J Bot 94(4): 526–532.
- Hammerlynn EP. 2001. Chlorophyll fluorescence and photosynthetic gas exchange responses to irradiance of Tree of Heaven (*Ailanthus altissima*) in contrasting urban environments. Photosynthetica 39(1):79–86.
- Heisey RM. 1997. Allelopathy and the secret life of *Ailanthus altissima*. Arnoldia (Jamaica Plain) 57(3): 28–36.
- Hoshovsky MC. 1999. Element stewardship abstract: *Ailanthus altissima* (tree of heaven). Arlington (VA): The Nature Conservancy.
- Hu SY. 1979. *Ailanthus*. Arnoldia 39:25–50.
- Illick JS, Brouse EF. 1926. The *Ailanthus* tree in Pennsylvania. Bulletin 38. Harrisburg (PA): Pennsylvania Department of Forests and Waters. 29 p.
- Knapp LB, Canham CD. 2000. Invasion of an old – growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. J Torrey Bot Soc 127:307–315.
- Kota NL. 2005. Comparative seed dispersal, seedling establishment and growth of exotic invasive *Ailanthus altissima* (Mill.) Swingle and native *Liriodendron tulipifera* (L.). Master's Thesis, West Virginia University, Morgantown, WV. 116 p.
- Kota NL, Landenberger RE, McGraw JB. 2006. Germination and early growth of *Ailanthus* and tulip poplar in three levels of forest disturbance. Bio Inv 9(2): 197–211.
- Kowarik I. 1995. Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. J Veg Sci 6:853–856.

- Lodge DM. 1993. Biological Invasions: Lessons for ecology. *Trends Ecol Evol* 8:133–137.
- McDonald RI, Urban DL. 2006. Edge effects on species composition and exotic species abundance in the North Carolina Piedmont. *Biol Inv* 8(5): 1049–1060.
- Miller JH. 1990. *Ailanthus altissima* In: Burns RM and Honkala BH (tech. cords.). *Silvics of North America Vol. 2 Hardwoods*. Agricultural Handbook 654. Washington (DC): U. S. Department of Agriculture, Forest Service. 877 p.
- NOAA. 2002. Ohio Climate Summary. <http://lwf.ncdc.noaa.gov/oa/climate/research/cag3/OH.html>
- Orwig DA, Abrams MD. 1994. Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: gap – obligate versus gap – facultative tree species. *Can J Forest Res* 24:2141–2149.
- Pan E, Bassuk N. 1985. Effects of soil compaction on the growth of *Ailanthus altissima* seedlings. *J Environ Hort* 3:158–162.
- Peigler R. 1993. A defense of *Ailanthus*. *Am Hort* 72(2):38–43.
- Pimentel D, Lach L, Zuniga R, Morrison D. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50(1):53–65.
- Rabe EP, Bassuk N. 1984. Adaptation of *Ailanthus altissima* to the urban environment through analysis of habitat usage and growth response to soil compaction. *Hortscience* 19(3):96.
- Richardson DM, Rouget M, Rejmanek M. 2004. Using natural experiments in the study of alien invasions: opportunities and limitations In: Gordon MS and Bartol SM (eds.) *Experimental Approaches to Conservation Biology*. Los Angeles, CA: The University of California Press. 358 p.
- Runkle JR. 1996. Central mesophytic forests In: Davis MB (ed.). *Eastern old-growth forests: prospects for rediscovery and recovery*. Washington (DC): Island Press. 383 p.
- Runkle JR, Fairbanks LA, Armstrong KH, Campbell TS, Espenschied-Reilly AL. 2005. Changes in older and younger woods in west-central Ohio. *Ohio J Sci* 105(5):116–124.
- Shah B. 1997. The checkered career of *Ailanthus altissima*. *Arnoldia* 57(3):21–27.
- Stein BA, Flack SR. 1996. *America's Least Wanted: Alien species invasions of U. S. ecosystems*. Arlington (VA): The Nature Conservancy. 31 p.
- Vitousek PM. 1990. Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57:7–13.
- Westman WE. 1990. Park management of exotic plant species: Problems and issues. *Conserv Biol* 4:251–260.
- Xheng H, Wu Y, Ding J, Binion D, Fu W, Reardon R. 2004. *Invasive plants of Asian origin established in the United States and their natural enemies*, Volume 1. Chinese Academy of Agricultural Sciences Institute of Biological Control, Beijing, 100081 P. R. China. USDA Forest Service, Forest Health Enterprise Team. Morgantown, WV 26505, U.S.A. United States Department of Agriculture Forest Service-FHTET 2004-05.
- Zar JH. 1999. *Biostatistical Analysis*, 4<sup>th</sup> ed. Upper Saddle River (NJ): Prentice Hall. 663 p.